CHAPTER 5

Benthic responses to sedimentation of phytoplankton on the Belgian Continental Shelf

Jan Vanaverbeke[1], Maria Franco[1], Dick van Oevelen[2], Leon Moodley[2], Pieter Provoost[2], Maaike Steyaert[1], Karline Soetaert[2] and Magda Vincx[1]

[1] Ghent University, Marine Biology Section, Krijgslaan 281/S8, B-9000 Gent, Belgium
[2] NIOO-CEME, Korringaweg 7, PO Box 140, 4400 AC Yerseke, The Netherlands

5.1 Introduction

The Belgian Continental Shelf (BCS), located in the nutrient enriched Southern Bight of the North Sea, is characterised by a high levels of primary production and algal biomasses (Lancelot *et al.*, 1987; Rousseau, 2000). Phytoplankton dynamics displays strong seasonal patterns with diatom blooms initiating the succession in February-March and the main spring bloom composed of diatoms and *Phaeocystis* in April-May (Rousseau *et al.*, 2002; 2008). At that time, *Phaeocystis* colonies can contribute up to 99% of the autotrophic biomass in the pelagic realm (Hamm & Rousseau, 2003). Phytoplankton summer blooms are mainly composed of diatoms which last as late as end October (Rousseau *et al.*, 2008). Although the bulk of phytoplankton production is mostly remineralized in the water column after the bloom (Rousseau *et al.*, 2000), still 24% is deposited on the sediment of the BCS, 65% of it being under the form of *Phaeocystis* colonies (Lancelot *et al.*, 2005).

Sedimentation of phytoplankton and derived matter, the phytodetritus, represents a major source of organic matter (OM) for the benthic system where it fuels benthic life (Graf, 1992). In return, benthic regeneration of nutrients is an important process for sustaining high rates of primary production in coastal areas (Nixon, 1980). The benthic response to phytoplankton sedimentation is however not unique. The receiving sediment type is a key factor determining the fate of freshly deposited OM. In fine-grained depositional areas, accumulation and sharp vertical profiles of labile OM can emerge after the phytodetritus sedimentation in spring (Steyaert *et al.*, 1999) and remineralisation can be delayed until late summer (Boon & Duineveld, 1998). On the contrary, rapid degradation of OM often takes place in coarser, permeable sediments (Ehrenhauss *et al.*, 2004; Janssen *et al.*, 2005; Bühring *et al.*, 2006). In these areas, tide induced lateral advective currents above the sediments prevent a mass sedimentation of phytodetritus (Huettel & Rush, 2000; Precht & Huettel, 2004). In addition, pore water is refreshed with tidal movement, keeping the

sediment oxygenated (Ziebis *et al.*, 1996; Janssen *et al.*, 2005) and removing the toxic by-products generated by remineralisation processes (Huettel *et al.*, 1998). All these factors accelerate the aerobic degradation of OM and the recycling of nutrients (Huettel & Rush, 2000; Janssen *et al.*, 2005; Bühring *et al.*, 2006) preventing the establishment of strong biogeochemical vertical profiles in these sediments.

Although the biogeochemical patterns in depositional and permeable sediments are well described and understood, little is known about the response of benthic organisms in sediments. The sediment distribution in the BCS shows contrasted areas with both fine-grained depositional areas and coarser, permeable sediments where this issue can be addressed. Two stations with contrasted sediments, Stn 115bis and Stn 330 (Figure 5.1), were therefore investigated in order to better understand how benthic organisms, from bacteria to macrobenthos, are responding to phytoplankton sedimentation.

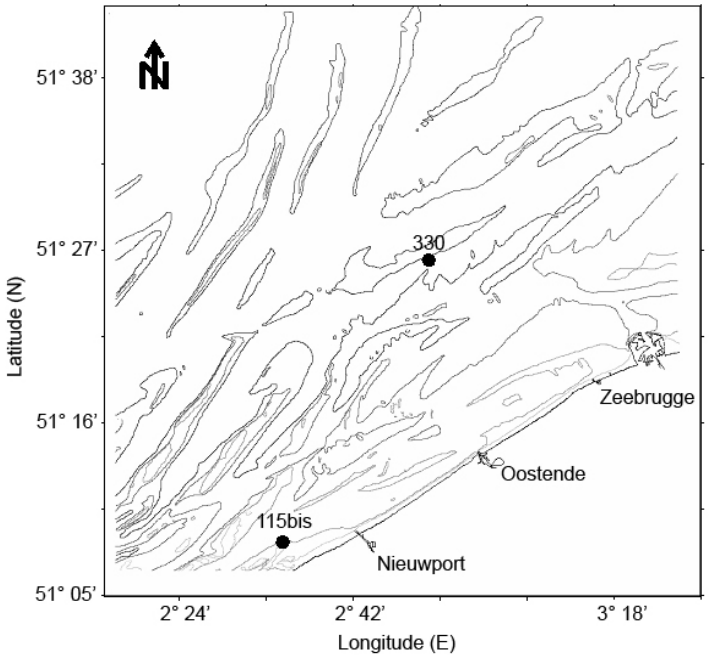


Figure 5.1. Location of the sampling Stn 115bis and Stn 330 of the BCS.

Stn 115bis is located close to the coast (51°09.2 N - 02°37.2 E; 13 m depth) and is characterized by fine sandy sediments according to the classification scale of Buchanan (1984) with a median grain size of 185 µm and a small fraction of mud (4%>63 µm; Steyaert, 2003). The sediment of Stn 330 (51°26.0 N - 02°48.5 E; 20 m depth), situated further off shore, is classified as medium sand (median grain size between 321 µm and 361 µm; Vanaverbeke *et al.*,

2004a) and has no mud. Both stations were intensively studied before, during and after the phytoplankton blooms in 1999 and 2003 in order to:

- describe the changes in the biogeochemical patterns;
- quantify the remineralisation processes;
- describe the response of the benthic organisms, *i.e.* bacteria, meiobenthos and macrobenthos, and;
- assess the relative importance of pelagic diatoms and *Phaeocystis* as food source for the benthos.

In this chapter, we compare the patterns and processes occurring in the two sediment types, focusing on the response of bacteria and nematodes. Nematodes are indeed the dominant taxon in the meiofauna, *i.e.* all metazoan animals passing a 1 mm but retained on a 38 µm sieve. Due their exclusively benthic life style, short generation times, high diversity and density, they are an ideal tool to reflect changes in the benthic environment (Kennedy & Jacoby, 1999).

5.2 Seasonal dynamics of phytodetritus sedimentation and mineralisation

5.2.1 Seasonal patterns of phytodetritus benthic distribution

Figure 5.2 compares the seasonal dynamics of phytoplankton, expressed as bulk Chlorophyll a (Chl *a*) in the surface and bottom waters at both Stn 115bis and Stn 330. The seasonal trend, with a well marked phytoplankton spring bloom and further moderate summer and fall outbursts, is similar to that found in other years (Steyaert, 2003; Vanaverbeke *et al.*, 2004 a,b; Franco *et al.*, 2007). As a general trend the similar Chl *a* concentrations measured in the surface and bottom water of both stations reflect the permanent well-mixed water column on the BCS. The higher Chl *a* maxima reached at the inshore Stn 115bis probably reflect the higher nutrient availability near the coast (Brion *et al.*, 2008; Rousseau *et al.*, 2008).

Sedimentation of phytodetritus can be estimated based on the integration of the Chl *a* concentration vertical profiles in the sediment column (Fig. 5.3). Sedimentation mainly occurs in April after the peak of the phytoplankton bloom (Fig. 5.2). Interestingly enough much higher sedimentary Chl *a* concentrations and a steeper vertical profile are observed in the fine sandy sediments of Stn 115bis (Fig. 5.3a). In contrast, the vertical Chl *a* profile in the medium sands at Stn 330 never displays such clear vertical gradient during the sampling period (Fig. 5.3b).

The oxygenation status in the sediments of the two stations is also different. The coarser sediments at Stn 330 remain completely oxic over the whole sediment column whereas at Stn 115bis anoxic sediments are observed just after the deposit of phytodetritus, and propagate from 0.4 cm sediment depth onwards. The lower Chl *a* concentrations, the full oxygenation and the absence

of steep vertical profiles reflect all together the permeable nature of the sediment at Stn 330, contrasting with the characteristics of a depositional sediment such as that of Stn 115bis.

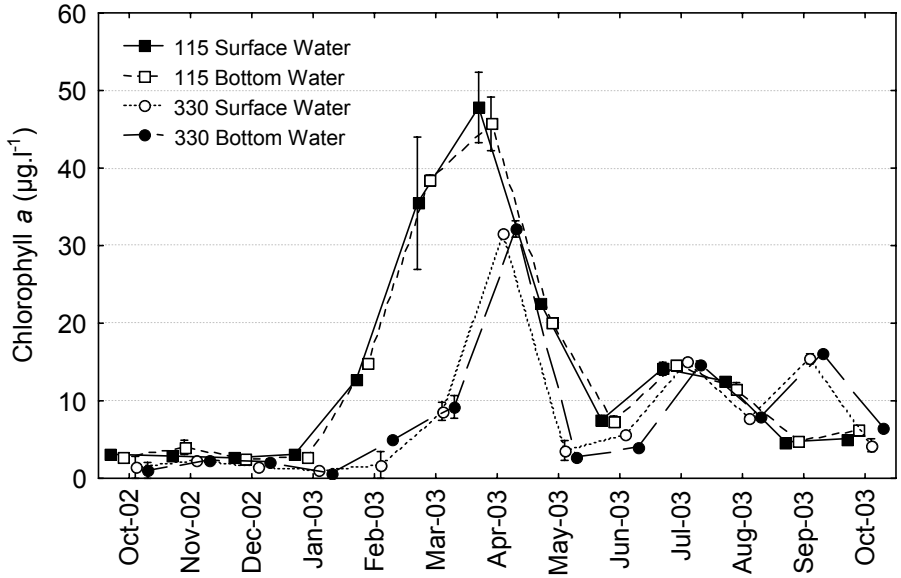
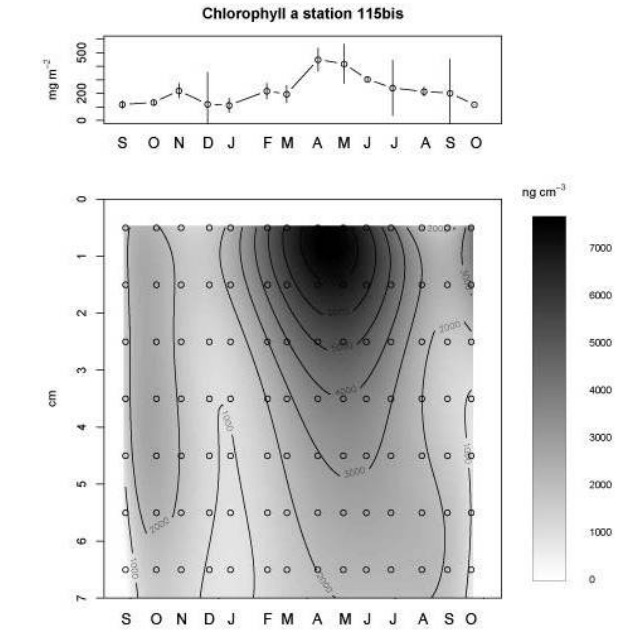


Figure 5.2. Chlorophyll *a* concentration (µg L-1) in the surface and bottom water at Stn 115bis and Stn 330 over the period October 2002-October 2003. Vertical bars represent the Standard Error. From Franco *et al.* (2007).

5.2.2 Seasonal patterns in mineralisation processes

The global mineralisation of the OM deposited to the sediment by the benthic community (bacteria, meiobenthos, macrobenthos) is generally estimated from the measurement of Sediment Oxygen Consumption (SOC) rates either *in situ* or under dark and temperature-controlled laboratory conditions (Moodley *et al.*, 1998). For this purpose, perspex cores with an internal diameter of 9.5 cm were sampled at both stations and transported to the laboratory, closed with a detachable lid containing an YSI 5739 oxygen electrode and a Teflon coated magnetic stirrer. The oxygen concentration in the water was then continuously monitored and SOC was calculated from the linear decrease of oxygen concentration over time (Moodley *et al.*, 1998).

a.



b.

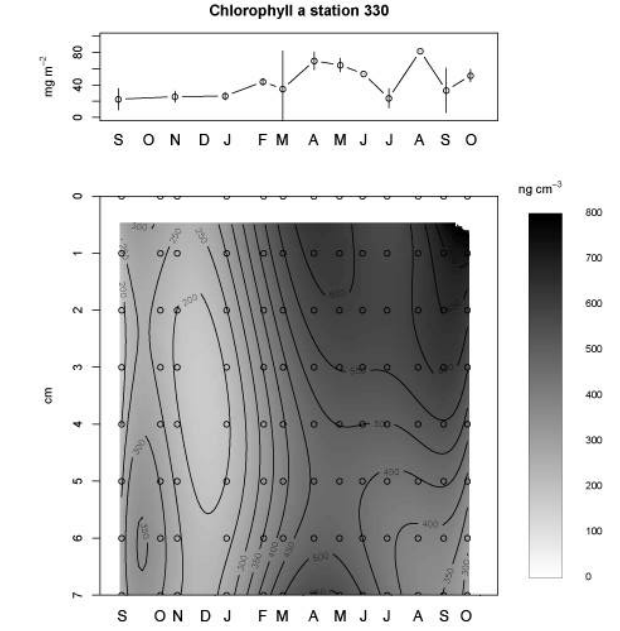


Figure 5.3. Vertical profiles of Chl *a* concentrations in the sediments (lower panels) and integrated Chl *a* concentrations in the sediment column (upper panels) of Stn 115bis (a) and Stn 330 (b) over the period October 2002 – October 2003.

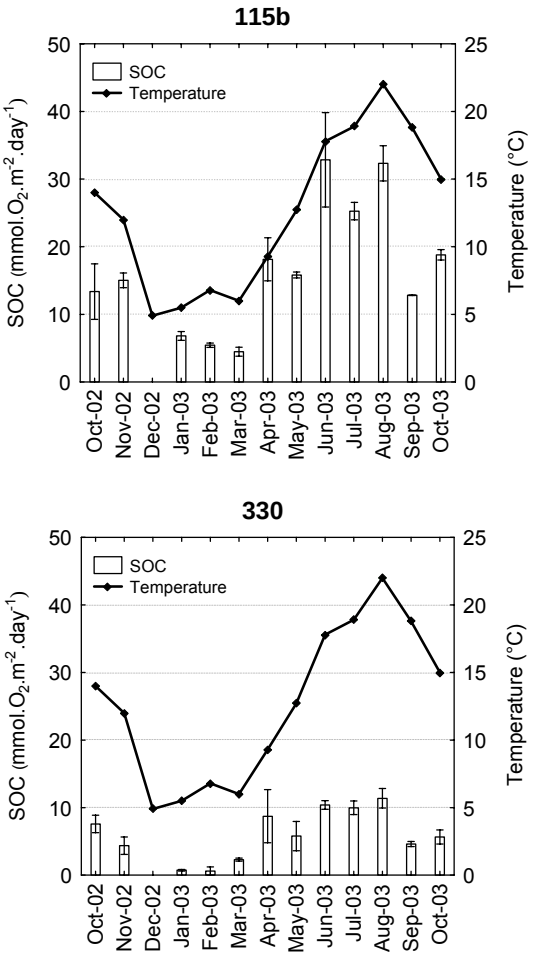


Figure 5.4. Sediment Oxygen Consumption (mmol O_2 m^{-2} d^{-1}) and water temperature (°C) at Stn 115bis and Stn 330 over the period October 2002-October 2003. The vertical bars represent the standard error.

As a general trend, SOC values calculated at Stn 115 bis were much higher than at Stn 330 at all sampling dates. This is due to the higher amount of phytodetritus deposited at the sediment surface of the fine sands of Stn 115bis than at Stn 330 (Fig. 5.3). At this latter station, surface primary production is lower and the higher bottom water currents above the seafloor prevent the deposition of the sedimenting phytodetritus (Franco *et al.*, 2007). In addition, SOC values measured at Stn 330 could well be underestimated due to the absence, in our laboratory experiments, of advective currents through these permeable sediments which prevents the continuous oxygenation of the sediment and removal of remineralisation byproducts. The absence of

porewater flow through the sediment can result in a SOC underestimation by a factor of 1.4, or even 2-3 when diatoms are added to experimental mesocosms (Ehrenhauss & Huettel, 2004). Even when taking this factor into account, SOC values measured for Stn 330 are lower than those recorded for St 115bis, but the difference is less obvious.

In both stations, SOC values were lowest in winter and increased after the phytodetritus sedimentation following the spring bloom. This suggests that in both sediment types, SOC is dependent on the quality and quantity of the available OM. In addition, the actual maximum SOC values calculated for the fine sediments of Stn 115bis are reached only 2 months (in June) after the main sedimentation event in April. This coincides with a drastic increase in water temperature (Fig. 5.4), suggesting that in fine sediments SOC is dependent on temperature as well (Provoost *et al.*, in preparation). This was not so clear at Stn 330, where values close to the maximum values were observed immediately after the arrival of phytodetritus to the seafloor, indicating that in permeable sediments, SOC rates are mainly dependent on the availability of degradable OM.

5.3 Benthic response to phytoplankton sedimentation

5.3.1 Bacterial communities

Marine benthic bacterial communities are known to react fast to OM deposition in terms of biomass production, cell division and activity which result in an increase in biomass, density and productivity (Graf *et al.*, 1982; Meyer-Reil, 1983; Goedkoop & Johnson, 1996; Boon *et al.*, 1998). This response is mainly influenced by the co-variation of OM supply and temperature (Graf *et al.*, 1982; Boon *et al.*, 1998; Van Duyl & Kop, 1994). Even though the bacterial response to sedimentation events in terms of biomass, density and productivity is well documented, little is known about possible changes in bacterial community composition and/or diversity. Changes in bacterial community composition were here investigated before, during and after a phytoplankton bloom at both stations and at two sediment depths, *i.e.* surface (0-1 cm) and sub-surface (4-5 cm). Denaturating Gradient Gel Electrophoresis (DGGE; Muyzer, 1999) was used after extraction of the bacterial DNA from the sediment following Dembo Diolla (2003) and Franco *et al.* (2007). Bacterial community composition was statistically analysed using a non-metric Multi Dimensional Scaling (MDS) which allows to group samples based on their similarity level. In the 2D ordination plot, samples characterized by similar bacterial communities are close to each other and reversely, are far away from one another when having very different communities. Figure 5.5 shows examples of DGGE gels and their corresponding statistical analysis. The MDS of bands shows that bacterial communities vary between stations, sediment depths and seasons (Franco *et al.*, 2007).

The bacterial community composition at both stations is significantly influenced by the Chl *a* concentration in the sediment, reflecting the importance of quantity and quality of OM (Franco *et al.*, 2007).

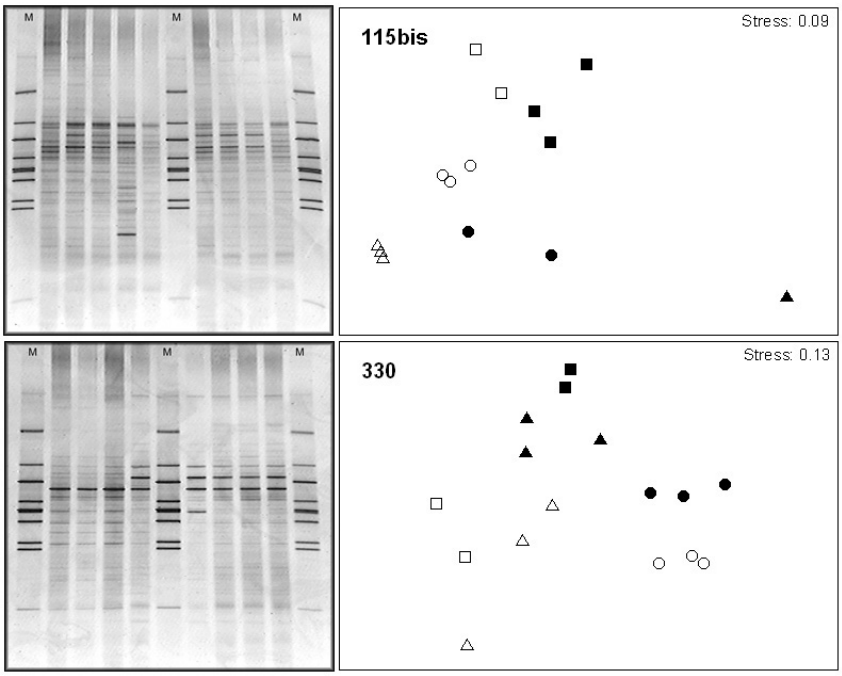


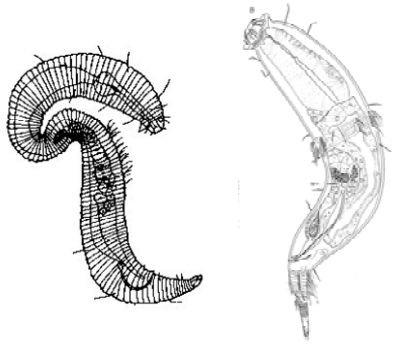
Figure 5.5. Example of DDGE gels and corresponding MDS analysis of bacterial community composition at Stn 115bis and Stn 330. Squares: February; triangles: April, circles: October. Open symbols: 0-1 com; solid symbols: 4-5 cm. Each band on the gels represents one Operational Taxonomical Unit. Redrawn from Franco *et al.* (2007).

Oxygen depletion resulting from OM mineralization might also contribute to the observed changes in bacterial communities (Janse *et al.*, 2000). Diversity was higher at the fine sediment station, probably due to the higher food availability and the co-existence of aerobic and anaerobic bacteria at that station. Bacterial community composition also varies with phytoplankton bloom stage, *i.e.* pre-bloom, bloom and post-bloom situation, suggesting an effect of phytoplankton sedimentation. The response of bacteria in terms of community composition is sediment-dependent and is influenced by local characteristics such as anoxia following OM sedimentation at Stn 115bis *vs* oxic sediment at Stn 330. Bacterial community composition and diversity is therefore regulated by food availability and quantity in combination with hydrodynamic stress and oxygenation.

5.3.2 Nematode communities

Nematode communities from both sites react differently to the OM sedimentation from the water column. The fastest response was observed at Stn 330 where nematode densities increase shortly after the sedimentation of the bloom, start decreasing already two months after the bloom and increase again during the moderate summer blooms (Fig. 5.7b; Franco *et al.*, 2007). The pattern of nematode density variation is similar to that observed in 1999 at Stn 330 where it was concomitant to an increase in nematode diversity

(Vanaverbeke *et al.*, 2004b). This seasonal distribution was attributed to an opportunistic response of an aberrant morphotype, the so-called stout nematodes (Fig. 5.6; Vanaverbeke *et al.*, 2004a) which are characterised by a length/width ratio <15 (Soetaert *et al.*, 2002).



Epsilonema *Richtersia*

Figure 5.6. Illustrations of *Epsilonema* sp. and *Richtersia* sp., two examples of stout nematodes.

Stout nematodes increase their densities at a much faster rate (6.5% d^{-1}) than that of the total community (1.5% d^{-1}) after the phytoplankton bloom deposition (Vanaverbeke *et al.*, 2004a). When OM is remineralised, which is a fast process due to the permeability of the sediment, the density decreases at a much faster rate as well (3% d^{-1}) compared to the total community (0.7% d^{-1}).This opportunistic behaviour can be explained by their small length (Vanaverbeke *et al.*, 2004a) which enables them to reach adulthood faster than the longer slender nematodes. As a consequence, they reproduce faster, triggering a fast increase in densities. Stout nematodes are however more sensitive to food shortage and starvation when OM is mineralised, dying earlier since smaller animals have a shorter life span (Kooijman, 1986). The increase in diversity was explained by the availability of a more wider variety of food particles (Vanaverbeke *et al.*, 2004b).

A different picture emerges at Stn 115bis where nematode densities increase gradually after the sedimentation event and reach maximum values in October (Fig. 5.7a; Steyaert, 2003; Franco, 2007). Contrary to Stn 330, no increase in diversity was observed (Steyaert, 2003). Increase in nematode densities is a consequence of successive reproduction periods of the dominant nematode species at well-defined sediment depths (Steyaert, 2003). The timing of nematode density increase at a given sediment depth coincides with the burial of phytodetritus, indicating that nematode species need a specific food quality to increase their densities. In addition to seasonal fluctuations, nematode densities also vary between stations (Fig. 5.7). Densities at Stn 115bis are always much higher in comparison with densities observed at St 330, which is a consequence of the higher availability of OM at Stn 115bis (Fig. 5.3).

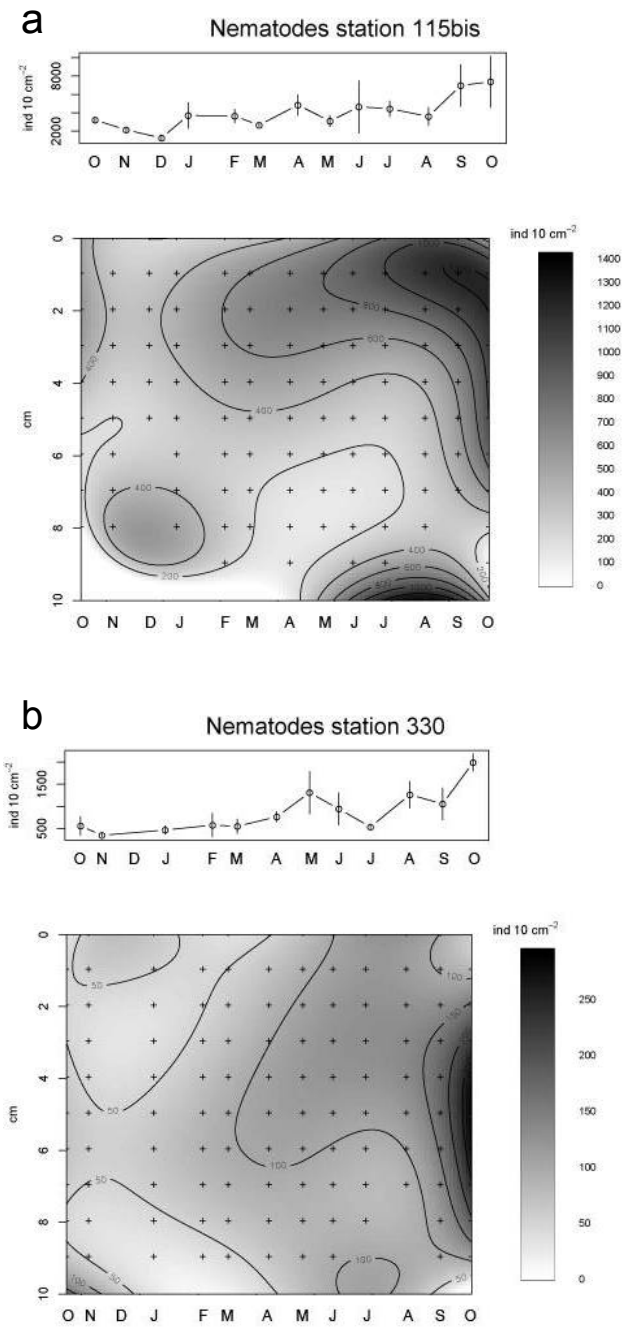


Figure 5.7. Vertical distribution of nematode total densities (lower panels) and average density in the sediment column (upper panels) at Stn 115bis (a) and Stn 330 (b) during the period October 2002 - October 2003. From Franco *et al.* (2007).

5.4 Phytodetritus as a food source for benthic organisms

5.4.1 Natural conditions

Stable isotopes ^{13}C and ^{15}N can be used to trace the food ingested by animals and hence to determine their trophic position. The ^{13}C of consumers is indeed a weighted average of the ^{13}C of their food sources whilst the ^{15}N signal increases of ± 3 ‰ at each trophic level (Post, 2002). During the seasonal cycle 2002-2003, ^{13}C and ^{15}N of particulate organic matter (POM) of the water column and the sediment and of meiobenthos were measured at three different periods, *i.e.* before (February), during (April) and after (October) the phytoplankton bloom. Meiobenthic organisms were picked from 2 depth layers, 0-1 cm and 4-5 cm (Franco, 2007). When possible, nematodes were identified at the genus level and the difference between stout and slender nematodes was made.

Measurements of $\delta^{13}C$ at Stn 115bis (Fig. 5.8) and at Stn 330 (Fig. 5.9) show, for both stations, different $\delta^{13}C$ values in the meiobenthic organisms and in the sediment POM, indicating that OM as a whole cannot be considered as an appropriate food source. Results show also little temporal fluctuation of the meiobenthos isotopic signature in the upper cm suggesting a constant food source throughout the year. These two observations suggest that the organisms living in the sediment surface depend on a constant but limited supply of fresh algal material originating from the water column (Franco *et al.*, 2008). The absence of vertical differences in the $\delta^{13}C$ values in the organisms from Stn 330 is due to the permeability of the sediment, suggesting that, at this station, the benthic food web is solely depending on fresh phytoplankton. At St 115bis, vertical differences in the $\delta^{13}C$ values in the nematodes except the genus *Richtersia* and *Sabatieria*, refered here as “other nematode”, reveal the use of different sources, with the deeper-dwelling nematodes being part of a food web based on older more fractionated and decomposed OM. These observations reflect the gradual burial and mineralisation process of fresh phytodetritus in finer sediments of Stn 115bis. The extremely low values of $\delta^{13}C$ measured in the benthic copepods in October suggest the existence, at Stn 115bis, of a chemoautotrophic food source based on sulphur-oxidising bacteria (Felbeck & Distel, 1999).

Except for copepods at Stn 115 bis in October 2003, $\delta^{15}N$ values show no significant differences between the meiobenthic taxa and within the nematodes (Franco *et al.*, 2008). This suggests that only limited predator-prey relationships exist within the meiobenthic community in our subtidal stations. Predatory nematodes were not dominant at the two sites (Steyaert 2003, Vanaverbeke *et al.*, 2004b) so that their higher $\delta^{15}N$ value could well be diluted in the “bulk nematode” value.

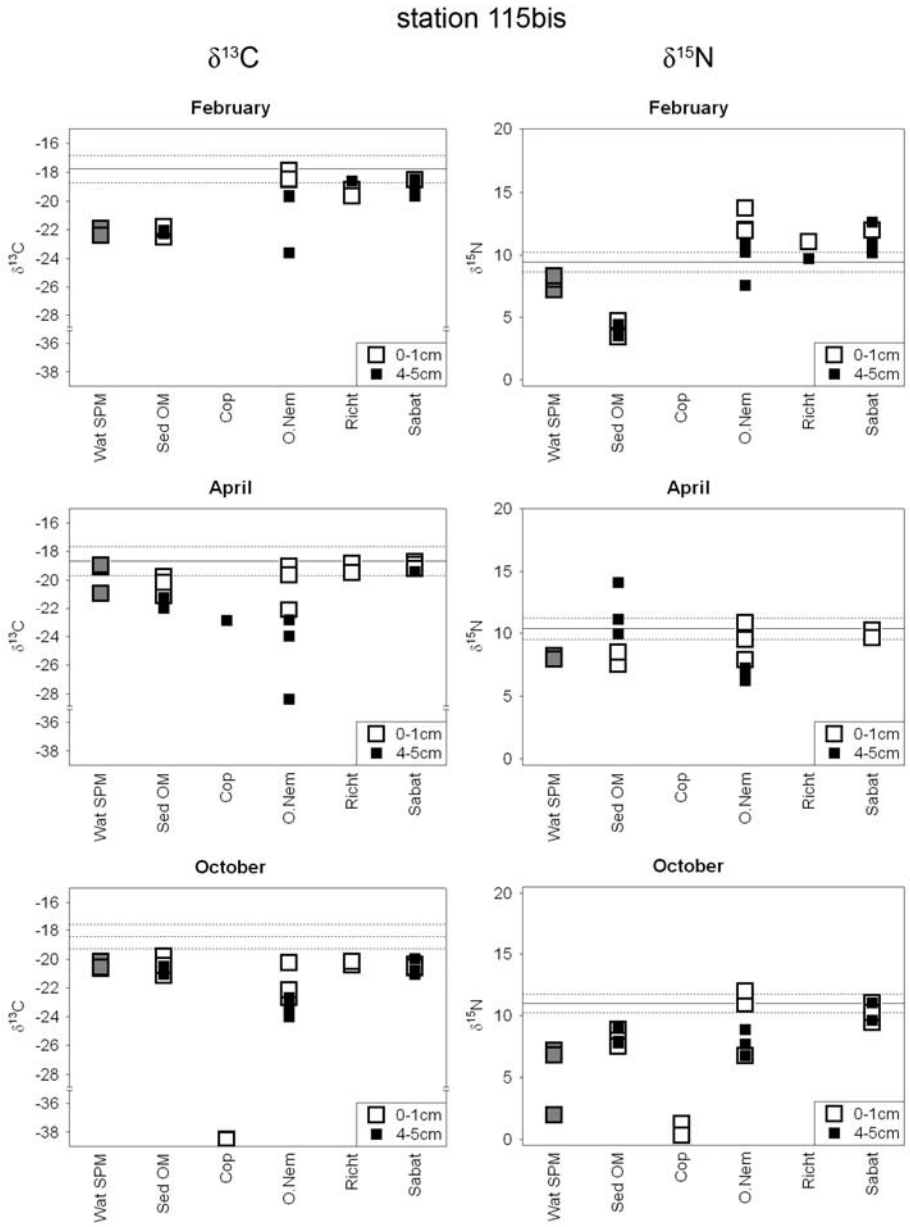


Figure 5.8. $\delta^{13}C$ (left panel) and $\delta^{15}N$ (right panel) signatures of water column (1 m above seafloor) suspended particulate matter (SPM), sediment OM and meiobenthic taxa at Stn 115bis. Horizontal line: mean (solid) and ± Standard Error (dotted) of $\delta^{13}C$ and $\delta^{15}N$ in benthic organisms in Stn 330. Organisms reported as Cop: copepods; O. Nem: other nematodes; Richt: *Richtersia*; Sabat: *Sabatieria.*

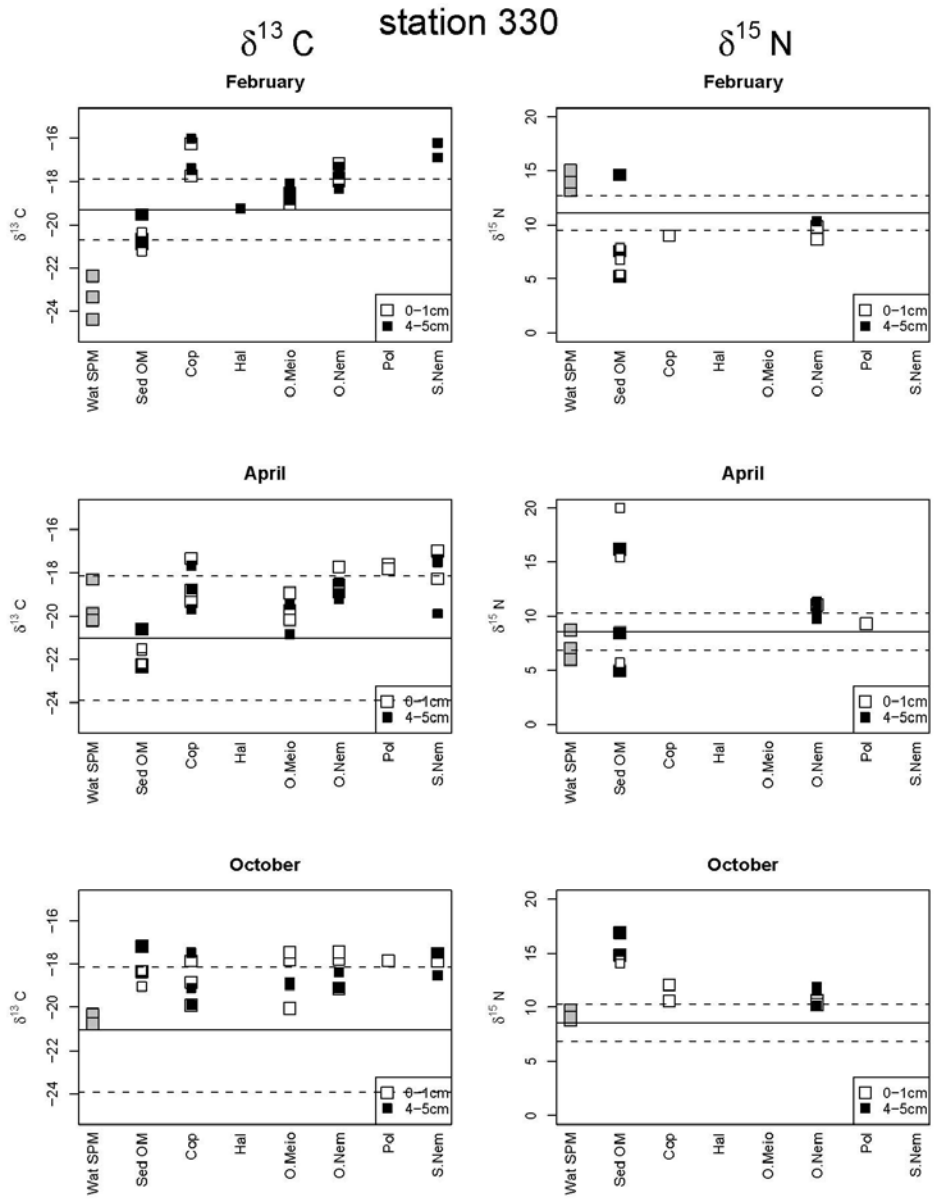


Figure 5.9. $\delta^{13}C$ (left panel) and $\delta^{15}N$ (right panel) signatures of water column (1 m above seafloor) suspended particulate matter (SPM), sediment OM and meiobenthic taxa at Stn 330. Horizontal line: mean (solid) and mean ± Standard Error (dotted) of $\delta^{13}C$ and $\delta^{15}N$ in benthic organisms at Stn 115bis. Organisms reported as Cop: copepods; Hal: Halacaroidea; O. Meio: other meiobenthos; O. Nem.: other nematodes; Pol: Polychaetes; St. Nem.: stout nematodes.

5.4.2 Planktonic diatoms and *Phaeocystis* as food source for the benthos

Although *Phaeocystis* is significantly contributing to the phytoplankton communities during spring (Rousseau *et al.*, 2000; 2008), the sedimentation of *Phaeocystis*-derived matter and its possible contribution as food resource for benthic organisms on the BCS is still unknown. So far, grazing on settled *Phaeocystis* colonies by benthic gastropods has been reported in tidal flats (Cadée, 1996), but no information on the trophic fate of *Phaeocystis* in the subtidal benthic ecosystem is available.

In order to resolve this question natural sediments sampled at Stn 115bis were incubated in presence of ^{13}C pre-labelled cultures of the diatom *Skeletonema costatum* (1000 mg C m^{-2}, 193 mg ^{13}C m^{-2}) and *Phaeocystis* (128 mg C m^{-2}, 50 mg ^{13}C m^{-2}) under laboratory-controlled conditions (see details in Franco *et al.*, in press). After two weeks, meiobenthic organisms from four sediment depths, 0-1, 1-3, 3-5 and 5-8 cm, were collected for isotope analysis (Fig. 5.10). Clearly the uptake of labelled phytoplankton was the highest in the upper cm-layer and was realized by the nematodes, the dominant taxon in the samples. *Phaeocystis* C uptake is one order of magnitude lower than *S. costatum* C uptake. On average over the whole core, some 0.20 ± 0.05% and 0.14 ± 0.02% of carbon added as *S. costatum* and *Phaeocystis,* respectively, were retrieved in the nematodes suggesting that both phytoplankton species enter the meiobenthic food web in low but comparable quantities.

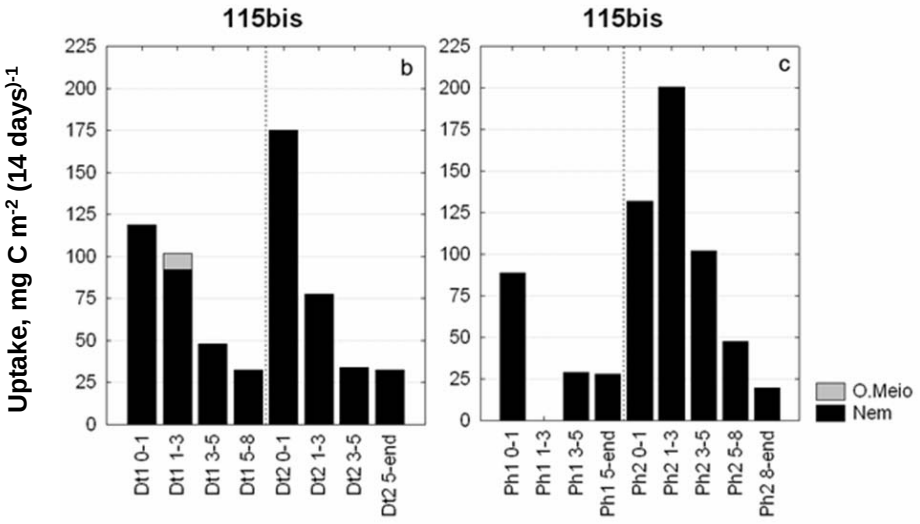


Figure 5.10. Total uptake (mgC m^{-2}) after 14 days of incubation of ^{13}C labelled diatoms *S. costatum* (left panel - Dt) and *Phaeocystis* (right panel - Ph) by nematodes (Nem) and other meiobenthos taxa (O. Meio) from Stn 115bis at 4 different sediment depths, 0-1, 1-3, 3-5 and 5-8 cm. Two replicates were performed for each treatment and depth. Note different Y-axis scaling (Redrawn from Franco, 2007).

When integrated over the sediment column and averaged over the incubation period, daily C uptake rates were estimated to 0.144 ± 0.033 and 0.014 ± 0.002 mgC m^{-2} d^{-1} in the *S. costatum* and *Phaeocystis* treatment respectively. This is largely unsufficient to sustain nematode C requirements as estimated from their respiration rates. These C uptake rates represent indeed only 0.66% (*S. costatum*) and 0.06% (*Phaeocystis*) of the C respired by nematodes (Franco *et al.*, in press). These experiments show that, although both *S. costatum* and *Phaeocystis* derived-carbon is consumed by nematodes, these organisms have to rely on other food sources to sustain their energy needs (Franco *et al.*, in press).

Although not important for nematodes, the role of both pelagic diatoms and *Phaeocystis* for the functioning of the benthic food web seems to important. Preliminary results reveal indeed that after 1 week, about 25% of C added as *S. costatum* and 10% of C added as *Phaeocystis* was respired in the benthic ecosystem in experimental microcosms (Moodley *et al.*, unpubl.).

5.5 Conclusions and perspectives

Our results show clearly that processes occurring in the sediment of the BCS are highly depending on the sedimentation of phytoplankton-derived material from the water column. However, the remineralisation is depending on the sediment type, which has a clear influence on the benthic response. When remineralisation is fast, as in permeable sediments, nematode densities increase fast after a sedimentation event. Although phytodetritus-derived carbon seems not to be the main food source for subtidal nematodes, animals inhabiting the surface of the sediments feed on freshly produced diatoms year-round.

In finer sediments, remineralisation is slower and more influenced by the water temperature, quality and quantity of the organic material. In these sediments, the organic loading is much higher and triggers anoxia during prolonged periods of the year. Nematode response in these sediments depends on the burial and degradation of organic matter and shows a time delay with respect to the peak sedimentation event. This coincides with the fact that different food sources were found at different depths at the fine sandy station. Both diatoms and *Phaeocystis* derived carbon is ingested by the benthic organisms, although diatoms are more important in the diet of the nematodes compared to *Phaeocystis*.

Future work should ideally focus on the role of the larger benthic animals, the macrofauna, in the mineralisation processes of the phytodetritus. Indeed, especially in the finer sediments, mineralisation processes and the response of the meiofauna to these processes is time-lagged with respect to the peak sedimentation event, and differs between sediment horizons. Macrobenthic activities such as bioturbation and bio-irrigation, greatly affect both the vertical distribution of organic matter and oxygen in the sediment. By altering the biogeochemical environment, these organisms have great influence on (1)

mineralisation rates of organic matter and (2) the availability of appropriate food sources for the meiobenthos.

5.6 References

Boon A.R. and G.C.A. Duineveld. 1998. Chlorophyll *a* as a marker for bioturbation and carbon flux in southern and central North Sea sediments. Marine Ecology Progress Series 162: 33-43

Boon A.R., Duineveld G.C.A., Berghuis E.M. and J.A. van der Weele. 1998. Relationships between benthic activity and the annual phytopigment cycle in near-bottom water and sediments in the Southern North Sea. Estuairne Coastal Shelf Science 46: 1-13

Brion N., Jans S., Chou L. and V. Rousseau. 2008. Nutrient loads to the Belgian Coastal Zone**.** In: Current Status of Eutrophication in the Belgian Coastal Zone. Rousseau V., Lancelot C. and D. Cox (Eds). Presses Universitaires de Bruxelles, Bruxelles, pp. 17-43

Buchanan J.B. 1984. Sediment analysis. In: Methods for the study of marine benthos. Holme N.A. and A.D. McIntyre (Eds). Blackwell Scientific Publications, Oxford and Edingburgh. 41-65

Bühring S.I., Ehrenhauss S., Kamp A., Moodley L. and U. Witte. 2006. Enhanced benthic activity in sandy sublittoral sediments: Evidence from C-13 tracer experiments. Marine Biology Research 2: 120-129

Cadée G.C. 1996. Accumulation and sedimentation of *Phaeocystis globosa* in the Dutch Wadden Sea. Journal of Sea Research 36: 321-327

Daro N., Breton E., Antajan E., Gasparini S. and V. Rousseau. 2008. Do *Phaeocystis* colony blooms affect zooplankton in the Belgian coastal zone? In: Current Status of Eutrophication in the Belgian Coastal Zone. V. Rousseau, C. Lancelot and D. Cox (Eds). Presses Universitaires de Bruxelles, Bruxelles, pp. 61-72

Demba Diallo M. 2003. Molecular study of the microbial community in pasture soil under *Acacia tortilis*_subsp. *Raddiana* and *Balanites aegyptica* in North Senegal. PhD thesis, Ghent University, Gent.

Ehrenhauss S. and M. Huettel. 2004. Advective transport and decomposition of chain-forming planktonic diatoms in permeable sediments. Journal of Sea Research 52: 179-197

Ehrenhauss S., Witte U., Buhring S.L. and M. Huettel. 2004. Effect of advective pore water transport on distribution and degradation of diatoms in permeable North Sea sediments. Marine Ecology Progress Series 271: 99-111

Felbeck H. And D.L. Distel. 1999. Prokaryotic Symbionts of Marine Invertebrates. In: The Prokaryotes: An Evolving Electronic Resource for the Microbiological Community. Dworkin M. *et al.* (Eds). 2nd edition, release 3.0, Springer-Verlag, New York

Franco M.A., De Mesel I., Demba Diallo M., van der Gucht K., Van Gansbeke D., Van Rijswijk P., Costa M.J., Vincx M. and J. Vanaverbeke. 2007. Impact of phytoplankton bloom deposition on benthic bacterial communities at two contrasting sediments in the Southern North Sea. Aquatic Microbial Ecology 48: 241-254.

Franco M.A., Soetaert K., Van Oevelen D., Van Gansbeke D., Costa M.J., Vincx M. and J. Vanaverbeke. 2008. Density, vertical distribution and trophic responses of metazoan meiobenthos to phytoplankton deposition in contrasting sediment types. Marine Ecology Progress Series 358:51-62

Franco M.A., Soetaert K., Costa M.J., Vincx M. and J. Vanaverbeke (in press). Uptake of phytodetritus by meiobenthos using ^{13}C labelled diatoms and *Phaeocystis* in two contrasting sediments from the North Sea. Journal of Experimental Biology and Ecology

Goedkoop W. and R.K. Johnson. 1996. Pelagic-benthic coupling: Profundal benthic community response to spring diatom deposition in mesotrophic Lake Erken. Limnology and Oceanography 41: 636-647

Graf G. 1992. Benthic-Pelagic Coupling - A Benthic View. Oceanogr Marine Biology 30: 149-190

Graf G., Bengtsson W., Diesner U., Schulz R. and H. Theede. 1982. Benthic response to sedimentation of a spring phytoplankton bloom - process and budget. Marine Biology 67: 201-208

Hamm C.E. and V. Rousseau. 2003. Composition, assimilation and degradation of *Phaeocystis globosa*-derived fatty acids in the North Sea. Journal of Sea Research 50: 271-283

Huettel M., Ziebis W., Forster S. And G.W. Luther. 1998. Advective transport affecting metal and nutrient distributions and interfacial fluxes in permeable sediments. Geochimica et Cosmochimica Acta 62: 613-631

Huettel M. and A. Rusch. 2000. Transport and degradation of phytoplankton in permeable sediment. Limnology and Oceanography 45: 534-549

Janse I., Zwart G., Van der Maarel M.J.E.C. and J.C. Gottschal. 2000. Composition of the bacteria community degrading *Phaeocystis* mucoplysaccharides in enrichment cultures. Aquatic Microbial Ecology 22: 119-133

Janssen F., Huettel M. And U. Witte. 2005. Pore-water advection and solute fluxes in permeable marine sediments (II): Benthic respiration at three sandy sites with different permeabilities (German Bight, North Sea). Limnology and Oceanography 50: 779-792

Kennedy A.D. and C.A. Jacoby. 1999. Biological indicators of marine environmental health: Meiofauna: a neglected benthic component. Environmental Monitoring and Assesment 54: 47-68

Kooijman S. 1986. Energy budgets can explain body size relations. Journal of Theoretical Biology 121: 269-282

Lancelot C., Billen G., Sournia A., Weisse T., Colijn F., Veldhuis M., Davies A. And P. Wassmann. 1987. *Phaeocystis* blooms and nutrient enrichment in the continental coastal zone of the North Sea. Ambio 16: 38-46

Lancelot C., Spitz Y., Gypens N., Ruddick K., Becquevort S., Rousseau V., Lacroix G. and G. Billen. 2005. Modelling diatom and *Phaeocystis* blooms and nutrient cycles in the Southern Bight of the North Sea: the MIRO model. Marine Ecology Progress Series 289: 63-78

Meyer-Reil L.A. 1983. Benthic response to sedimentation events during autumn to spring at a shallow-water Station in the western Kiel Bight 2. Analysis of benthic bacterial-populations. Marine Biology 77: 247-256

Moodley L., Heip C.H.R. and J.J. Middelburg. 1998. Benthic activity in sediments of the northwestern Adriatic Sea: sediment oxygen consumption, macro- and meiofauna dynamics. Journal of Sea Research 40: 263-280

Muyzer G. 1999. DGGE/TGGE a method for identifying genes from natural ecosystems. Current Opinion in Microbiology 2: 317-322

Nixon S.W. 1980. Between coastal marshes and coastal waters: A review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. In: Estuarine and Wetland Processes. Hamilton P. and K.B. MacDonald (Eds). Plenum Press, New York. Pp 437–525

Precht E. and H. Huettel. 2004. Rapid wave-driven advective pore water exchange in a permeable coastal sediment. Journal of Sea Research 51: 93-107

Rousseau V. 2000. Dynamics of *Phaeocystis* and diatom blooms in the eutrophicated coastal waters of the Southern Bight of the North Sea. Ph.D. thesis. Université Libre de Bruxelles. 205 pp.

Rousseau V., Becquevort S., Parent J.-Y., Gasparini S., Daro M.-H., Tackx M. and C. Lancelot. 2000. Trophic efficiency of the planktonic food web in a coastal ecosystem dominated by *Phaeocystis* colonies. Journal of Sea Research 43: 357-372

Rousseau V., Leynaert A., Daoud N. and C. Lancelot. 2002. Diatom succession, silicification and silicic acid availability in Belgian coastal waters (Southern North Sea). Marine Ecology Progress Series 236: 61-73

Rousseau V., Park Y., Ruddick K., Vyverman W., Jans S. and C. Lancelot. 2008. Phytoplankton blooms in response to nutrient enrichment. In: Current Status of Eutrophication in the Belgian Coastal Zone. Rousseau V., Lancelot C. and D. Cox (Eds). Presses Universitaires de Bruxelles, Bruxelles, pp. 45-59

Soetaert K., Muthumbi A. and C.H.R. Heip. 2002. Size and shape of ocean margins nematodes: morphological diversity and depth-related patterns. Marine Ecology Progress Series 242:179–193

Steyaert M. 2003. Spatial and temporal scales of nematode communities in the North Sea and Westerschelde. PhD thesis, Ghent Univeristy, 114 pp.

Steyaert M., Garner N., Van Gansbeke D. and M. Vincx. 1999. Nematode communities from the North Sea: environmental controls on species diversity and vertical distribution within the sediment. Journal of the Marine Biological Association of United Kingdom 79:253-264

Vanaverbeke J., Soetaert K. And M. Vincx. 2004a. Changes in morphometric characteristics of nematode communities during a spring phytoplankton bloom deposition. Marine Ecology Progress Series 273: 139-146

Vanaverbeke J., Steyaert M., Soetaert K., Rousseau V., Van Gansbeke D., Parent J.-Y., and M. Vincx. 2004b. Changes in structural and functional diversity of nematode communities during a spring phytoplankton bloom in the southern North Sea. Journal of Sea Research 52: 281-292

Van Duyl F.C., Kop A.J. 1994. Bacterial production in North-Sea sediments - Clues to seasonal and spatial variations. Marine Biology 120: 323-337

Ziebis W., Huettel M. And S. Forster. 1996. Impact of biogenic sediment topography on oxygen fluxes in permeable seabeds. Marine Ecology Progress Series 140: 227-237